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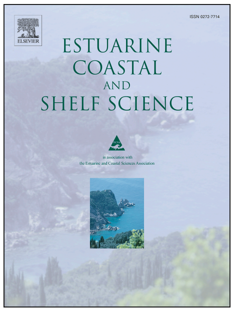

Short-term losses and long-term gains: The non-native species *Austrominius modestus* in Lough Hyne Marine Nature Reserve

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Abstract

The non-native barnacle species *Austrominius modestus* was first recorded in Ireland, close to Lough Hyne marine nature reserve in 1957. This species was not

recorded inside the Lough until 1980, but by 2001 was the dominant intertidal barnacle within the reserve. It has been suggested that increases in the abundance of this species at other locations in Europe may be linked to increasing sea surface temperatures, and that *A. modestus* is an "ecological sleeper". Despite an overall trend for increasing sea surface temperatures, this long term warming is punctuated by extreme events such as severely cold winters. *A. modestus* is warm water adapted, and has been recorded to decrease in abundance following cold winters. The winters of 2009/2010 and 2010/2011 were amongst the coldest recorded in Ireland in past decades. In the present study, higher levels of mortality were recorded for *A. modestus* than native barnacle species in Lough Hyne following these cold winters. Additionally, this species was recorded at lower abundances at the majority of sites surveyed in Lough Hyne in 2011 compared with 2009. Despite this, *A. modestus* remains the dominant barnacle species in the Lough and monitoring the recruitment of intertidal barnacles within Lough Hyne during 2014-2015 revealed that *A. modestus* was the most abundant recruit at study sites, both in removal plots and in the pre-existing community. The year-round breeding of *A. modestus* in addition to the closed nature of the Lough promotes *A. modestus* within the reserve. Despite this, native barnacle species continue to persist in Lough Hyne, though generally at low abundances, with the exception of exposed locations such as the Rapids and Bullock Island where natives outnumber *A. modestus*. The future intertidal barnacle community within the Lough is likely to be dominated by *A. modestus* with *Chthamalus montagui* and *C. stellatus* being abundant at sites which are not suitable for *A. modestus*. While the consequences of this are unknown, it is possible that the presence of *A. modestus* may alter trophic interactions and energy flow within the reserve.

KEYWORDS: *Austrominius modestus*, barnacle, climate, invasive, marine reserve, long term monitoring

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Abstract

The non-native barnacle species *Austrominius modestus* was first recorded in Ireland, close to Lough Hyne marine nature reserve in 1957. This species was not recorded inside the Lough until 1980, but by 2001 was the dominant intertidal barnacle within the reserve. It has been suggested that increases in the abundance of this species at other locations in Europe may be linked to increasing sea surface temperatures, and that *A. modestus* is an "ecological sleeper". Despite an overall trend for increasing sea surface temperatures, this long term warming is punctuated by extreme events such as severely cold winters. *A. modestus* is warm water adapted, and has been recorded to decrease in abundance following cold winters. The winters of 2009/2010 and 2010/2011 were amongst the coldest recorded in Ireland in past decades. In the present study, higher levels of mortality were recorded for *A. modestus* than native barnacle species in Lough Hyne following these cold winters. Additionally, this species was recorded at lower abundances at the majority of sites surveyed in Lough Hyne in 2011 compared with 2009. Despite this, *A. modestus* remains the dominant barnacle species in the Lough and monitoring the recruitment of intertidal barnacles within Lough Hyne during 2014-2015 revealed that *A. modestus* was the most abundant recruit at study sites, both in removal plots and in the pre-existing community. The year-round breeding of *A. modestus* in addition to the closed nature of the Lough promotes *A. modestus* within the reserve. Despite this, native barnacle species continue to persist in Lough Hyne, though

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1. Introduction

Austrominius (=*Elminius*) *modestus* (Darwin) is an Australasian barnacle species, which was first recorded in Britain in the early 1940s (Bishop, 1947; Crisp and Chipperfield, 1948). It is now widespread on European coasts (O'Riordan, 1996; Allen *et al.,* 2006; Arenas *et al.,* 2006; Tøttrup *et al.,* 2010), favouring sheltered and estuarine locations (Moore, 1944; Southward, 1955; Crisp, 1958). *A. modestus* reproduces during the entire year via continuous broods (Moore, 1944; Crisp and Davies, 1955; Moyse, 1960; Patel and Crisp, 1960; Moyse, 1963), while native barnacle species have more restricted breeding seasons (Burrows *et al.,* 1992; Anderson, 1994). The first record of *A. modestus* in Ireland was in 1957, close to Lough Hyne (Beard, 1957), though it is believed to have been established in Cork Harbour prior to this (O'Riordan, 2002), likely between 1954 and 1956 (Crisp and Southward, 1959).

Lough Hyne was the first designated statutory marine reserve in Europe and remains Ireland's only marine reserve (Anon, 1981a; Anon, 1981b). The fauna and flora of Lough Hyne have been extensively studied for almost a century (Kitching, 1987) and long-term datasets exist for many species within the Lough, including barnacles. Survey work within the Lough during 1955 and 1958 did not record *A. modestus*, but found that *Chthamalus stellatus* (not yet divided into *Chthamalus montagui* Southward and *Chthamalus stellatus* (Poli)) and, to a lesser extent, *Semibalanus balanoides* (Linnaeus) were widespread (Ebling *et al.,* 1960). It was not until 1980 that *A. modestus* was recorded within Lough Hyne (Holmes, 1980), shortly before its designation as a marine reserve. In the early 1990s, Little *et al.* (1992) reported that over-all barnacle cover had increased in the Lough since surveys carried out by Ebling *et al.* (1960), due to the introduction of *A. modestus* and increases in the abundance of *S. balanoides*, which coincided with a cooling period from the 1960s to the 1980s (Hiscock *et al.*, 2004).

By 2001, *A. modestus* was recorded as the dominant barnacle within the Lough, and the sole species of intertidal barnacle found at some locations there (Lawson *et al.,* 2004). Increases in the abundance of *A. modestus* were also reported from other locations in Europe during this time period (Franke and Gutow, 2004; Simkanin *et al.,* 2005; Reichert and Buchholz, 2006; O'Riordan *et al.,* 2009; Gomes-Filho *et al.,* 2010; Witte *et al.,* 2010), some of which were linked to increasing sea surface temperatures (Lawson *et al.,* 2004; Witte *et al.,* 2010). While there has been a general warming trend in the North-East Atlantic since the 1980s, it has been particularly marked since the 1990s, with a rise of 1°C in seawater temperature recorded the English Channel during the last decade of the twentieth century (Hawkins *et al.*, 2003).

Witte *et al.* (2010) suggested that *A. modestus* could be an "ecological sleeper", a species that survives in an area, but does not become abundant there until environmental conditions - increasing air and seawater temperatures in the case of *A. modestus* - become favourable. Like many invasive species, *A. modestus* is warm water adapted (Witte *et al.,* 2010), with a physiological optimum above 20°C (Harms, 1999), suggesting that this invasive species will continue to proliferate with predicted increasing air and seawater temperatures over the next century (IPCC, 2014). However, as seen from temperatures recorded during the last century, despite overall warming trends, cold periods may occur (Hiscock *et al.*, 2004) and additionally, extreme events, such as cold winters, interrupt this long-term warming (Wang *et al.,* 2010; Wethey *et al.,* 2011). It has long been recognised that temperature is a key factor in determining the distribution of species, and extreme winter or summer temperatures can limit the abundance of species at their range limits (Hutchins, 1947). There have been reports of cold events having a negative impact on the abundance of *A. modestus*, with low recruitment and survival recorded following cold winters (den Hartog, 1953; Crisp, 1964; Harms and Anger, 1989; Witte *et al.,* 2010).

Intertidal organisms such as barnacles experience climatic conditions of both air and sea, and so have been identified as good indicators of climate change (Simkanin *et* *al.,* 2005; Helmuth *et al.,* 2006; Hawkins *et al*., 2008). The relative abundance of warm and cold water adapted barnacle species has even been used as a descriptor of temperature trends (Southward, 1991; Simkanin *et al.,* 2005). The aims of the present study were to determine whether the cold winters of 2009/2010 and 2010/2011 had any impact on the abundance of the invasive species and to describe the current status of *A. modestus* in Lough Hyne by monitoring the recruitment and survival of recruits at four sites within the marine reserve during 2014-2015.

2. Materials and Methods

2.1 Study site

Lough Hyne Marine Nature Reserve (51°30'N, 9°18'W) is a marine lough located in County Cork, on the south-west coast of Ireland. It measures 0.8 km x 0.6 km and is connected by a narrow channel called the Rapids to Barloge Creek, which opens into the Atlantic (Kitching, 1987) (Figure 1). The rapids are approximately 150m long, 12m wide and less than 1m deep at low water, resulting in an asymmetrical tidal pattern (4 hour flood and 8.5 hour ebb). The tidal range within the Lough is less than 1.5m, compared with one of >4m on the adjacent Atlantic coastline (Bassindale *et al.,* 1948) and the reduced intertidal zone within the Lough is generally sheltered (De Grave and Holmes, 1998). Castle Island partially divides the Lough into northern and southern basins. The Western Trough is the deepest part of the Lough, reaching depths of almost 50m. The Lough has an overall flushing time of twenty-two tidal cycles (Johnson *et al*., 1995) and salinity within Lough Hyne is similar to the adjacent coastal Atlantic (Watson *et al.,* 2005).

2.2 Barnacle abundance

Twenty-one sites in the marine reserve (seventeen within the Lough itself and four outside the Lough) were surveyed between April and August 2009 (Figure 1; Table 1), seventeen of which had previously been surveyed by Lawson *et al.* (2004). Sites varied in terms of current flow, macroalgal cover, freshwater input and substrate (natural or artificial). However, all sites had a vertical aspect. At each site, three line transects (approximately 1m apart) were surveyed. Along each transect, a 10cm x 10cm quadrat was used in a vertical, contiguous manner, so that each quadrat survey area represented a 10cm vertical drop in shore height. The number of individuals of each barnacle species present in each quadrat was recorded. Newly metamorphosed individuals were also identified and counted, as were individuals growing inside cracks and crevices. However, individuals growing on mobile animals, such as limpets, were not recorded.

Following the cold winters of 2009/2010 and 2010/2011, in the summers of 2010 and 2011, five of these sites (Barloge Quay, Kelly's Pier, Goleen, North Labra and Whirlpool Cliff) were resurveyed. The five sites were selected based on their geographical spread, in addition to environmental conditions present at each site. The same methodology as the 2009 survey was used, however any recently dead barnacles (shell intact, but operculum partly or completely absent) were also recorded. Due to difficulties in distinguishing *Chthamalus stellatus* from *Chthamalus montagui* with missing opercular plates, both species were recorded as *Chthamalus* spp. In addition, these five sites and the remaining sites that had been surveyed in

2009, were resurveyed between May and July 2011, following the same methodology as used in the 2009 survey.

2.3 Barnacle recruitment

Monitoring of barnacle recruitment on natural substrata in the pre-existing community and in the presence of free space was carried out between April 2014 and April 2015 in the Marine Reserve. Four sites (Whirlpool Cliff, Goleen Cliff, Northwest Castle and Barloge Creek) were selected for monitoring due to the presence of a vertical rock face suitable for the establishment of monitoring plots and a pre-existing barnacle community consisting of both *A. modestus* and native barnacle species. In February 2014, three removal and three control plots were established at areas approximate to the high, mid and low shore at each site (n = 9 of each plot type per site). Removal plots measured $25cm^2$ and were created by clearing the plot area of all organisms, plus an additional edge of 1cm on each side of the plot, using a paint scraper. To ensure that all organisms had been removed, the rock surface was then scoured using wire wool. To allow for continued monitoring of the re-colonisation of these plots over time, the location of the plot was marked on the rock surface using a red paint mark. On each monthly field visit, the top left hand corner of a $25cm^2$ quadrat was aligned with the paint mark, and a photograph was taken of the plot area using a Nikon Coolpix AW10 digital camera in macro mode. From these images the recruitment and survival of different barnacle species was determined. Control plots also measured $25cm^2$ but were not manipulated in any way, control plot location was marked using green paint. The amount of free space present within each control plot was calculated by estimating the percentage cover of bare rock within the plot and converting this to area (cm^2). This was done using an acetate sheet with a grid of dots, at a density of 4 dots cm^{-2}. A density of 0.5 dots $25cm^{-2}$ has been shown to give consistent and reproducible estimates of percentage cover (Littler *et al.,* 1986), however given the small size of the organisms in this study a higher density was chosen. This acetate sheet was then placed over a laptop screen with the image of the plot area enlarged to "full screen". The number of dots that were above an area of bare rock was counted, and divided by the total number of dots covering the plot area, to calculate percentage cover. The number of recruits in each control plot could then be converted to represent number of recruits $25cm^{-2}$ of free space, to allow for comparison with removal plots.

2.4 Temperature data

Long term data relating to the air and sea temperatures were obtained from Met Éireann. Mean minimum and mean maximum air temperatures were recorded at Sherkin Island weather station and mean monthly sea surface temperatures were recorded by buoys M3 and M5 off the south coast of Ireland. Seawater temperatures within the Lough were recorded using fixed temperature recorders on buoys in the north basin and south basin at a depth of 3.6m. Maximum, minimum and mean temperatures were available for the periods June 2009 – June 2010, June 2010 – December 2010 and from December 2010 – July 2011.

2.5 Statistical Analysis

Statistical analysis was carried out using R Studio software 3.3.0 (R Core Team, 2016). The 'prop.test' function was used to compare the percentage mortality of each species at each site in 2010 and 2011. Barnacle recruitment during 2014 – 2015 was in the form of count data, with a high amount of zeros. To account for this, a zero inflated model with a negative binomial distribution was constructed. A negative binomial distribution was chosen as it was found to have significantly better fit for the data than a Poisson distribution (Vuong's test, $p < 0.01$). Model validation was carried out by plotting the model residuals against the fitted values and QQ – plots.

3. Results

3.1 2009 barnacle survey

Austrominius modestus was the only barnacle species recorded at all twenty-one survey sites during the 2009 survey and was the sole barnacle species found at two sites in the North Basin of the Lough. *A. modestus* was recorded as the most abundant species at eighteen of the survey sites. At the remaining three sites, which were located within the Rapids and outside the Lough at Bullock Island, native species were dominant. *Semibalanus balanoides* and *Chthamalus stellatus* were recorded at much higher abundances at these latter three locations than at the other survey sites. *C. montagui* was the most abundant native barnacle species recorded during the 2009 survey. While it was recorded at relatively high abundances at many sites within the Lough, highest abundances for this species were also recorded at sites within the Rapids (Table A.1).

3.2 Abundance estimates at five sites in 2009, 2010 and 2011

A. modestus was the most abundant species at each of the five sites in all three years and was the sole barnacle species recorded at Kelly's Pier in 2009 and 2011 (Figure 2). Highest abundances of *A. modestus* were recorded at Whirlpool Cliff, with a maximum mean abundance of 161.5 (± 42.70) ind. dm^{-2} in 2009 (Figure 2). Lowest abundances of this species were recorded at Barloge Quay in each of the three years, with a maximum of 4.6 (± 1.42) ind. dm^{-2} recorded in 2010 (Figure 2). Highest densities of *A. modestus* were recorded across all five sites in 2009, with lower densities recorded at Kelly's Pier, Goleen Cliff and Whirlpool Cliff in 2010. Lowest abundances of this species were recorded at all sites in 2011.

S. balanoides was recorded at lower abundances than the other native barnacle species, *C. montagui* and *C. stellatus* at most sites within the Lough in all years (Figure 2). The highest mean abundance of this species was recorded at Whirlpool Cliff in 2010 (28.7 ± 7.83 ind. dm^{-2}) and although it had decreased in abundance at this location by 2011, it remained more abundant than the other two native species at this site (Figure 2). At Barloge Quay, *S. balanoides* was more abundant than *C. montagui* or *C. stellatus* in all three years; with a maximum of 2.2 (± 0.83) ind. dm^{-2} in 2010 (Figure 2). Higher mean abundances of *S. balanoides* were recorded at all sites in 2010 in comparison with 2009, with the exception of Goleen Cliff (Figure 2). A decrease in abundance was recorded for this species at all five sites between 2010 and 2011, with mean abundances equal to or lower than those initially recorded in 2009 observed at all sites except Whirlpool Cliff (Figure 2).

Highest mean abundances of *C. montagui* were recorded at North Labhra during each survey year, with a maximum mean abundance of 18.0 (± 7.75) ind. dm^{-2} recorded here in 2010. *C. stellatus* was most abundant at Goleen Cliff in all three years, with a maximum mean abundance of 14.6 (± 5.60 ind. dm^{-2}) in 2010 (Figure 2). Higher mean abundances of both *C. montagui* and *C. stellatus* were recorded across all sites in 2010 in comparison with 2009, with the exception of *C. montagui* at Whirlpool Cliff (Figure 2). Following this a decrease in mean abundance was recorded for *C. stellatus* at all sites in 2011. *C. montagui* was recorded at higher mean abundances at Goleen Cliff and Whirlpool Cliff in 2011 in comparison with 2010, however it had decreased in mean abundance at the remaining three sites (Figure 2).

3.3 Mortality recorded in summer 2010 and 2011

Levels of mortality varied with species, site and year. In 2010, *A. modestus* exhibited a higher level of mortality than the native species at most sites, ranging from 3% at Kelly's Pier to 13% at Goleen Cliff. At Barloge Quay native species had higher levels of mortality than *A. modestus* with 29% mortality recorded for *Chthamalus* spp. and 13% for *S. balanoides* (Figure 3). In 2011 higher levels of mortality were recorded for *A. modestus* than for native barnacle species at all five sites, with levels ranging from 7% at Kelly's Pier to 55% at Barloge Quay for the non-native species. Highest levels of mortality for native species were also recorded at Barloge Quay, with 38% mortality recorded for *S. balanoides* and 44% for *Chthamalus* spp., while no mortality was recorded for the native species at Kelly's Pier (Figure 3).

A significantly higher level of mortality was recorded for all species at all sites in 2011 in comparison with 2010 (Table A.2), with the exception of *S. balanoides* at Whirlpool Cliff (not significant) and *A. modestus* at Goleen Cliff, where levels of mortality were significantly higher ($p < 0.001$) in 2010. Although a lower level of mortality was recorded for *S. balanoides* at Whirlpool Cliff in 2011 (0%) than 2010 (<1%) (Figure 3), this difference was not statistically significant (Table A.2).

3.4 2011 Survey

A. modestus was again recorded at all twenty-one survey sites in 2011, but was recorded at lower abundances at eighteen sites in comparison with 2009. *A. modestus* remained the most abundant barnacle species at twelve of the survey sites and was again the sole species recorded at Kelly's Pier in the North Basin of the Lough. *A. modestus* was the least abundant barnacle species at survey sites within the Rapids and outside the Lough at Dromadoon and Bullock Island (Table A.3).

C. montagui was present at nineteen of the survey sites, absent from Kelly's Pier and Goleen. This species was the most abundant species at eight of the survey sites and exhibited increases in abundance at ten sites in comparison with the 2009 survey. *C. stellatus* was recorded at fifteen of the survey sites and was recorded as the most abundant species at the Top of the Rapids, displaying a large increase in abundance since the 2009 survey. Both Chthamalid species were recorded at highest abundances at sites in the Rapids, and outside the Lough at Dromadoon and Bullock Island (Table A.3).

S. balanoides was the least abundant of all barnacle species, however it was recorded at seventeen sites in 2011 in comparison with eleven in 2009. Despite being recorded at more locations it was only found at very low abundances <1 ind. dm^{-2} at the majority of sites. Highest abundances of *S. balanoides* were recorded at Whirlpool Cliff and outside the Lough in the Rapids, Dromadoon and Bullock Island (Table A.3).

3.5 Temperature

Monthly mean sea surface temperatures for coastal waters ranged from 9.35°C in March 2010 to 16.3°C in August and September 2010 (Figure 4). Mean seawater temperatures recorded within the Lough were higher than those of coastal waters, with the period of June 2009 – June 2010 having a mean seawater temperature of 13.55°C. Mean maximum and mean minimum air temperatures were lower in January 2010 and 2011 in comparison with the same months in 2009 (Figure 4). Lowest mean minimum air temperatures were recorded in January 2010 and December 2010 (1.1°C). Lowest mean maximum air temperatures were also recorded in the same months (7.8°C and 6.7°C respectively). Highest mean maximum and mean minimum air temperatures were recorded during June, July and August 2010 (max: 18.2°C – 19.2°C, min: 12.1°C – 12.8 °C) (Figure 4).

3.6 Recruitment in 2014-2015

Recruits of *A. modestus* were recorded at all four study sites, while those of *S. balanoides* were absent from Northwest Castle and *C. montagui* recruits were not recorded at Barloge Creek (Figures 5 and 6). No recruits of *C. stellatus* were recorded in experimental plots during this study. Overall, recruits of *A. modestus* were significantly more abundant than those of *S. balanoides* ($p < 0.001$) or *C. montagui* ($p < 0.001$) (Table A.4).

A closely-similar trend in recruit abundance was observed in both removal and control plots at all four study sites, although recruits of all three species were more abundant in control plots (Figure 6) than removal plots ($p < 0.001$) (Figure 5). Recruits of *A. modestus* were significantly more abundant than both *S. balanoides* and *C. montagui* in both plot types ($p < 0.001$) (Figures 5 and 6; Table A.4). *C. montagui* was the least abundant recruit in both plot types ($p < 0.001$), with a maximum density of 2.08 (± 0.94) ind. 25 cm^{-2} recorded from control plots (Figure 6) and 0.33 (± 0.13) ind. 25 cm^{-2} in removal plots (Figure 5). Maximum density of *S. balanoides* recruits recorded was 5.81 (± 3.43) ind. 25 cm^{-2} in control plots (Figure 6) and 1.99 (± 1.44) ind. 25 cm^{-2} in removal plots (Figure 5). *A. modestus* recruits were recorded at a maximum density of 32.61 (± 14.59) ind. 25 cm^{-2} in control plots (Figure 6) and 9.96 (± 3.88) ind. 25 cm^{-2} in removal plots (Figure 5).

Significantly lower abundances of recruits were recorded at Barloge Creek in comparison with the three sites within the Lough itself ($p < 0.001$) (Figures 5 and 6; Table A.4). *S. balanoides* recruits were initially dominant in both plot types at this site, but ultimately *A. modestus* recruits outnumbered native species in both plots types at this site (Figures 5 and 6). *A. modestus* recruits peaked in abundance in June 2014 and following this maintained a stable level of abundance until the end of the study (Figure 5 and 6). A slight peak in the abundance of *S. balanoides* recruits was observed between May 2014 and July 2014 at Barloge Creek (both plot types) (Figures 5 and 6) and Whirlpool Cliff (control plots) (Figure 6).

4. Discussion

Austrominius modestus remains the dominant barnacle species within Lough Hyne Marine Nature Reserve. The non-native species was recorded at all survey sites during this study and was present at some locations where native species were not recorded. This is in keeping with the findings of Lawson *et al.* (2004), who also reported the dominance of *A. modestus* in Lough Hyne, in particular at sites with freshwater influence in the Northern Basin of the Lough. Interestingly, since the Lawson *et al.* (2004) study, *A. modestus* has not entirely displaced native species in the intertidal zone at any additional locations in Lough Hyne. Native barnacle species remain present at the majority of survey sites within the marine reserve, though often at low abundances in comparison with *A. modestus*. In the present study, highest abundances of native barnacle species were recorded at sites outside the Lough and in the Rapids, which was also the case in 2001 (Lawson *et al.,* 2004).

The winter of 2009/2010 has been recorded as one of the coldest winters on record in the northern hemisphere (Wang *et al.*, 2010) and temperature data from Met Éireann shows that air and sea temperatures during the following winter of 2010/2011 were on average slightly colder than 2009/2010 on the south coast of Ireland. The asymmetrical tidal cycle within Lough Hyne means that intertidal barnacles spend more time emersed than immersed, and so are subject to cold winter air temperatures for long periods of time (Little and Trowbridge, 2010). In one particular area of the Lough, Goleen, a blanket of white snow/ice was observed on the water during the winter of 2009/2010 for the first time in over forty years (T. Kearney and T. Kelly pers. obs.). Higher levels of mortality were recorded for *A. modestus* than native barnacle species in both 2010 and 2011 and this species was recorded to decrease in abundance at the majority of survey sites between 2009 and 2011. It is important to note that baseline data regarding normal levels of mortality for these species in Lough Hyne is not available for comparison, however in terms of these particular cold-event years, *A. modestus* displayed higher levels of mortality than the native species.

Cold winter events have previously been linked with high levels of mortality and low levels of recruitment for *A. modestus* at other locations within its invaded range (den Hartog, 1953; Crisp, 1958; Crisp, 1964; Harms and Anger, 1989; Witte *et al.,* 2010). It is predicted that there will be an increase in the frequency of cold winters in the coming years, due to negative NAO events (Wang *et al.*, 2010), which may have a limiting effect on the abundance of *A. modestus.* Other invasive species have also been negatively impacted by cold events in their invaded ranges, for example Thieltges *et al.* (2004) reported mass mortality of the invasive slipper limpet (*Crepidula fornicata*) in the Wadden Sea during the cold winters of 2000/2001 and 2001/2002. The invasive mussel, *Perna viridis*, was also observed to undergo a mass mortality event in the southeast United States during the winter of 2009/2010 (Firth *et al.,* 2011). Even if direct mortality from cold events does not occur, exposure to periods of extreme cold can induce sublethal effects or stress (Urian *et al.,* 2010) which can impact on survival and reproduction, potentially limiting invasive species.

The cold winters of 2009/2010 and 2010/2011 were expected to have favoured the cold adapted *Semibalanus balanoides*. Despite displaying an increase in abundance between 2009 and 2010 due to the presence of new recruits, subsequently there was a decrease in the abundance of the species between 2010 and 2011. Given that a lag phase of approximately two years is often exhibited between changes in temperature and subsequent changes in population densities for *S. balanoides* (Southward, 1967), it is possible that a longer time interval was required to observe any population increases. It would be interesting to investigate differences in recruitment success of both *S. balanoides* and *A. modestus* in years following cold winters, to understand the long term impacts that cold events have on populations of the native and non-native species. It is also possible that the abundance of adult *S. balanoides* within the Lough is insufficient to promote a population increase. Import of larvae from waters outside the Lough may be required for significant population growth, though the low flushing time within the Lough, in particular in the North Basin (Bassindale *et al.,* 1957), make this unlikely.

The low abundance of *S. balanoides* in 2011 at sites where it had been absent during the 2009 survey illustrates the unlikelihood of *S. balanoides* population growth. Despite being present, abundances were very low, with only a few individuals recorded at each site. As *S. balanoides* is a cross fertilising hermaphorodite (Barnes and Crisp, 1956; Rainbow, 1984), those individuals present would need to be in close proximity to allow them to breed, ensuring further increases in abundance. The future survival of *S. balanoides* is not certain at Lough Hyne, despite species generally having a lower risk of extinction in marine reserves (Lubchenco *et al.,* 2003). It has been found that the contraction of the southern range limit of *S. balanoides* in Europe is linked to warm winter temperatures that inhibit reproduction (Wethey and Woodin, 2008) and *S. balanoides* population declines have previously been observed during warm periods which favour *C. montagui* (Southward and Crisp, 1954; Southward, 1967; Southward, 1991; Hawkins *et al.,* 2008, Hawkins *et al.*, 2009, Mieszkowska *et al.*, 2014). Although the occurrence of occasional cold winter events may favour *S. balanoides*, the low abundance of adults within the Lough could preclude recruitment at high densities here. The increase in *C montagui* abundance recorded at some sites between surveys carried out in 2009 and 2011 may be attributed to the lack of competitive pressure from *S. balanoides* (Connell, 1961, Poloczanska *et al*., 2008, Mieszkowska *et al*., 2014), favourable temperatures during the summer and early autumn, when this species is breeding (Burrows, 1992) or the over-arching trend of increasing temperatures promoting this species (Poloczanksa *et al.*, 2008, Mieskowska *et al*., 2014) despite some adult mortality recorded following the cold winters.

Recruits of *A. modestus* were dominant at the three survey sites within the Lough in 2014-2015, however recruits of at least one native barnacle species were also recorded in both removal and control plots at all sites. Ultimately, *A. modestus* also became dominant at Barloge Creek, located outside the Lough, despite *S. balanoides* recruits being more abundant here initially. The pattern of recruitment observed in removal plots and in the surrounding community was very similar and the creation of free space did not promote the abundance of *A. modestus*. The ability of *A. modestus* to reproduce throughout the entire year (O'Riordan and Murphy, 2000) via continuous broods (Moore, 1944; Crisp and Davies, 1955; Moyse, 1960; Patel and Crisp, 1960; Moyse, 1963), in addition to the low flushing time in the Lough contribute to high abundances of *A. modestus* (Jessopp and McAllen, 2008). Larvae of this species have been found to be more abundant inside Lough Hyne than waters outside the reserve (Jessopp and McAllen, 2007) and *A. modestus* has been noted to be more successful inside the marine reserve than in non-protected areas (Burfeind *et al.,* 2013). It is possible that juvenile stages of *A. modestus* may be constantly present within the waters of the Marine Reserve, which could act as a reservoir for this non-native species. Jessopp and McAllen (2009) found no net export of *A. modestus* larvae from the reserve, likely due to the presence of the rapids and long retention time of the Lough, which limit connectivity to the adjacent coastline (Jessopp, 2007; Jessopp and McAllen, 2007). This is important given the potential for marine reserves to act as exporters of larvae to surrounding waters (Jessopp and McAllen 2007; Hoskin *et al.,* 2010), potentially playing a role in the spread of invasive species.

A. modestus remains the dominant barnacle within Lough Hyne, although native barnacles continue to persist. Natives are generally present at low densities, but are dominant at some locations within the Lough that are not suitable for *A. modestus*. Despite its abundance, Watson *et al.* (2005) stated that this invasive species had "little discernible effect" on native species at this location, while Lawson *et al.* (2004) noted that, while the impact of *A. modestus* in Lough Hyne remains unclear, it is likely to cause ecological harm. Non-native species have the potential to compromise marine protected areas as they alter the ecosystem or reduce biodiversity (Bax *et al.,* 2003). As suspension feeders, barnacles are responsible for the transfer of energy between overlying waters and the intertidal community (Baird *et al.,* 2012). Ecological Network Analysis carried out by Baird *et al.* (2012) in the Sylt-Rømø Bight of the North Sea examined the effects of *A. modestus* and the non-native oyster *Crassostrea gigas* on native ecosystem structure and function. They found that the presence of the invasive species had impacts on lower trophic levels, mainly affecting phytoplankton abundance. A similar effect is possible in Lough Hyne. The potential presence of *A. modestus* larvae within the plankton throughout the entire year, due to the production of continuous broods, could also alter trophic dynamics within the system, having knock-on effects at multiple trophic levels. Despite displaying higher levels of mortality than native barnacle species and decreasing in abundance following cold winter events, *A. modestus* continues to be the dominant intertidal barnacle in Lough Hyne and is likely to remain so as it recruits so successfully here. Climatic warming, despite being punctuated by extreme cold events, is likely to produce an intertidal community composed of *A. modestus*, *C. montagui* and *C. stellatus*. The impact that this may have on energy flow and trophic interactions in the Lough warrants future investigation, especially given its status as a marine reserve.

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References

Allen, B.A., Power, A.M., O'Riordan, R.M., Myers, A.A. and McGrath, D. (2006) Increases in the abundance of the invasive barnacle *Elminius modestus* Darwin in Ireland. Proceedings of the Royal Irish Academy 106B(2): 155-161

Anderson, D.T. (1994) Barnacles: Structure, function, development and evolution. *Chapman and Hall, London.* 1st Edition

Anon (1981a) Nature Reserve (Lough Hyne) regulations, 1981. Statutory instrument No. 2907 of 1981. Stationery Office, Dublin

Anon (1981b) Nature Reserve (Lough Hyne) establishment order, 1981. Statutory instrument No. 206 of 1981. Stationery Office, Dublin

Arenas, F., Bishop, J.D.D., Carlton, J.T., Dyrynda, P.J., Farnham, W.F., Gonzalez, D.J., Jacobs, M.W., Lambert, C., Lambert, G., Nielsen, S.E., Pederson, J.A., Porter, J.S., Ward, S. and Wood, C.A. (2006) Alien species and other notable records from a rapid assessment survey of marinas on the south coast of England. Journal of the Marine Biological Association of the United Kingdom 86: 1329-1337

Baird, D., Asmus, H. and Asmus, R. (2012) Effect of invasive species on the structure and function of the Sylt-Rømø Bight ecosystem, northern Wadden Sea, over three time periods. Marine Ecology Progress Series 462: 143-162

Barnes, H. and Crisp, D.J. (1956) Evidence of self-fertilisation in certain species of barnacles. Journal of the Marine Biological Association of the United Kingdom 35: 631-639

Bassindale, R., Ebling, F.J., Kitching, J.A. and Purchon, R.D. (1948) The ecology of Lough Hyne Rapids with special reference to water currents. Journal of Ecology 36(2): 305-322

Bassindale, R., Davenport, E., Ebling, F.J., Kitching, J.A., Sleigh, M.A. and Sloane, J.F. (1957) The ecology of the Lough Ine Rapids with special reference to water currents. VI. Effects of the Rapids on the hydrography of the South Basin. Journal of Ecology 45: 879-900

Bax, N., Williamson, A., Aguero, M., Gonzalez, E. and Geeves, W. (2003) Marine invasive alien species: a threat to global biodiversity. Marine Policy 27: 313-323

Beard, D.M. (1957) Occurrence of *Elminius modestus* Darwin in Ireland. Nature 23: 1145

Bishop, M.W.H. (1947) Establishment of an immigrant barnacle in British coastal waters. Nature 159: 501-502

Burfeind, D.D., Pitt, K.A., Connolly, R.M. and Byers, J.E. (2013) Performance of non-native species within marine reserves. Biological Invasions 15, 17-28

Burrows, M.T., Hawkins, S.J. and Southward, A.J. (1992) A comparison of reproduction in co-occurring chthamalid barnacles, *Chthamalus stellstus* (Poli) and *Chthamalus montagui* Southward. Journal of Experimental Marine Biology and Ecology 160: 229-249

Connell, J.H. (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42: 710–723

Crisp, D.J. (1958) The spread of *Elminius modestus* Darwin in North-West Europe. Journal of the Marine Biological Association of the United Kingdom 37: 483-520

Crisp, D.J. (1964) The effects of the severe winter of 1962-63 on marine life in Britain. Journal of Animal Ecology 33(1): 165-210

Crisp, D.J. and Chipperfield, P.N.J. (1948) Occurrence of *Elminius modestus* (Darwin) in British waters. Nature 161: 64

Crisp, D.J. and Davies, P.A. (1955) Observations *in vivo* on the breeding of *Elminius modestus* grown on glass slides. Journal of the Marine Biological Association of the United Kingdom 34: 357-380

Crisp, D.J. and Southward, A.J. (1959) The further spread of *Elminius modestus* in the British Isles to 1959. Journal of the Marine Biological Association of the United Kingdom 38: 429-437

De Grave, S. and Holmes, J.M.C. (1998) The distribution of marine isopoda (Crustacea) in Lough Hyne. Biology and Environment: Proceedings of the Royal Irish Academy 98B(1): 23-30

den Hartog, C. (1953) Immigration, dissemination and ecology of *Elminius modestus* Darwin in the North Sea, especially along the Dutch coast. Beaufortia 4: 9-20

Ebling, F.J., Sleigh, M.A., Sloane, J.F. and Kitching, J.A. (1960) The ecology of Lough Ine: VII. Distribution of some common plants and animals of the littoral and shallow sublittoral regions. Journal of Ecology 48(1): 29-53

Firth, L.B., Knights, A.M. and Bell, S.S. (2011) Air temperature and winter mortality: Implications for the persistence of the invasive mussel, *Perna viridis* in the intertidal zone of the south-eastern United States. Journal of Experimental Marine Biology and Ecology 400: 250-256

Franke, H.D. and Gutow, L. (2004) Long-term changes in the macrozoobenthos around the rocky island of Helgoland (Germna Bight, North Sea). Helogoland Marine Research 58: 303-310

Gomes-Filho, J.G.F., Hawkins, S.J., Aquino-Souza, R. and Thompson, R.C. (2010) Distribution of barnacles and dominance of the introduced species *Elminius modestus* along two estuaries in South-West England. Marine Biodiversity Records 3: 1-11

Harms, J. (1999) The neozoan *Elminius modestus* Darwin (Crustacea, Cirripedia): Possible explanations for its successful invasion in European water. Helgoländer Meeresuntersuchungen 52: 337-345

Harms, J. and Anger, K. (1989) Settlement of the barnacle *Elminius modestus* Darwin on test panels at Helgoland (North Sea): A ten year study. Topics in Marine Biology 53(2): 417-421

Hawkins, S.J., Southward, A.J. and Genner, M.J. (2003) Detection of environmental change in a marine ecosystem – evidence from the western English Channel. The Science of the Total Environment 310: 245-256

Hawkins, S.J., Moore, P.J., Burrows, M.T., Poloczanska, E., Mieszkowska, N., Herbert, R.J.H., Jenkins, S.R., Thompson, R.C., Genner, M.J. and Southward, A.J. (2008)

Complex interactions in a rapidly changing world: responses of rocky shore communities to recent climate change. Climate Research 37: 123-133

Hawkins, S.J., Sugden, H.E., Mieszkowska, N., Moore, P.J., Poloczanska, E., Leaper, R., Herbert, R.J.H., Genner, M.J., Moschella, P.S., Thompson, R.C., Jenkins, S.R., Southward, A.J. and Burrows, M.T. (2009) Consequences of climate-driven biodiversity changes for ecosystem functioning of North European rocky shores. Marine Ecology Progress Series 396: 245-259

Helmuth, B., Mieszkowska, N., Moore, P. and Hawkins, S.J. (2006) Living on the edge of two changing worlds: Forecasting the responses of rocky intertidal ecosystems to climate change. Annual Review of Ecology, Evolution and Sytematics 37: 373-404

Hiscock, K., Southward, A., Titley, I. and Hawkins, S. (2004) Effects of changing temperature on benthic marine life in Britain and Ireland. Aquatic Conservation: Marine and Freshwater Ecosystems 14: 333-362

Holmes, J.M.C. (1980) Some crustaceans from Lough Ine, Co. Cork. Bulletin of the Irish Biogeographical Society 4: 33-40

Hoskin, M.G., Coleman, R.A., von Carlhausen, E. and Davis, C.M. (2010) Variable population responses by large decapod crustaceans to the establishment of a temperate marine no-take zone. Canadian Journal of Fisheries and Aquatic Sciences 68: 185-200

Hutchins, L.W. (1947) The bases for temperature zonation in geographical distribution. Ecological Monographs 17(3): 325-335

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Jessopp, M. (2007) The quick and the dead: larval mortality due to turbulent tidal transport. Journal of the Marine Biological Association of the United Kingdom 87: 675-680

Jessopp, M.J. and McAllen, R.J. (2007) Water retention and limited larval dispersal: implications for short and long distance dispersers in marine reserves. Marine Ecology Progress Series 333: 27-36

Jessopp, M.J. and McAllen, R.J. (2008) Go with the flow: tidal import and export of larvae from semi-enclosed bays. Hydrobiologia 606: 81-92

Johnson, M.P., Costello, M.J. and O'Donnell, D. (1995) The nutrient economy of a marine inlet: Lough Hyne, south west Ireland. Ophelia 41: 137-151

Kitching JA (1987) Ecological studies at Lough Hyne. Academic Press.

Lawson, J., Davenport, J. and Whitaker, A. (2004) Barnacle distribution in Lough Hyne Marine Nature Reserve: a new baseline and an account of invasion by the introduced Australasian species *Elminius modestus* Darwin. Estuarine, Coastal and Shelf Science 60: 729-735

Little, C. and Trowbridge, C.D. (2010) Intertidal and shallow subtidal monitoring: Report to the National Parks and Wildlife Service. Permit numbers R12/10 and R42-45/10

Little, C., Morritt, D. and Stirling, P. (1992) Changes in the shore fauna and flora of Lough Hyne. The Irish Naturalists' Journal 24(3): 87-95

Littler, M.M., Littler, D.S., Blair, S.M. and Norris, J.N. (1986) Deep-water plant communities from an unchartered sea mount off San Salvador Island, Bahamas: distribution, abundance and primary productivity. Deep-Sea Research 33(7): 881-892

Lubchenco, J., Palumbi, S.R., Gaines, S.D. and Andelman, S. (2003) Plugging a hole in the ocean: the emerging science of marine reserves. Ecological Applications 13(1): S3-37

Mieszkowska, N., Burrows, M.T., Pannacciulli, F.G. and Hawkins, S.J. (2014) Mulitdecadal signals within co-occurring intertidal barnacles *Semibalanus balanoides* and *Chthamalus* spp. linked to the Atlantic Multidecadal Oscillation. Journal of Marine Systems 133: 70-76

Moore, L.B. (1944) Some intertidal sessile barnacles of New Zealand. Transactions of the Royal Society of New Zealand 73: 315-334

Moyse, J. (1960) Mass rearing of barnacle cyprids in the laboratory. Nature 185: 120

Moyse, J. (1963) A comparison of the value of various flagellates and diatoms as food for barnacle larvae. Journal du Conseil 28: 175-187

O'Riordan, R.M. (1996) The current status and distribution of the Australian barnacle *Elminius modestus* in Ireland. In: Irish Marine Science 1995, Keegan BF and O'Connor R (Eds.) Galway University Press Ltd.

O'Riordan, R.M. (2002) The accidental introduction of marine animals into Ireland. Biological Invaders: the impact of exotic species. Royal Irish Academy, Dublin, 96-106

O'Riordan, R.M. and Murphy, O. (2000) Variation in the reproductive cycle of *Elminius modestus* in southern Ireland. Journal of the Marine Biological Association of the United Kingdom 80: 607-616

O'Riordan, R.M., Culloty, S., Davenport, J. and McAllen, R. (2009) Increases in the abundance of the invasive barnacle *Austrominius modestus* on the Isle of Cumbrae, Scotland. Marine Biodiversity Records 2: 1-4

Patel, B. and Crisp, D.J. (1960) The influence of temperature on the breeding and moulting activities of some warm-water species of operculate barnacles. Journal of the Marine Biological Association of the United Kingdom 39: 667-680

Poloczanska, E.S., Hawkins, S.J., Southward, A.J. and Burrows, M.T. (2008) Modeling the response of populations of competing species to climate change. Ecology 89: 3138-3149

R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/

Rainbow, P.S. (1984) An introduction to the biology of British littoral barnacles. Field Studies 6: 1-51

Reichert, K. and Buchholz, F. (2006) Changes in the macrozoobenthos of the intertidal zone at Helgoland (German Bight, North Sea): a survey of 1984 repeated in 2002. Helgoland Marine Research 60: 213-223

Simkanin, C., Power, AM., Myers, A., McGrath, D., Southward, A., Mieszkowska, N., Leaper, R. and O'Riordan, R. (2005) Using historical data to detect temporal changes in the abundances of intertidal species on Irish shores. Journal of the Marine Biological Association of the United Kingdom 85: 1329-1340

Southward, A.J. (1955) On the behaviour of barnacles. I. The relation of cirral and other activities to temperature. Journal of the Marine Biological Association of the United Kingdom 34: 403-422

Southward, A.J. (1967) Recent changes in abundance of intertidal barnacles in South-West England: a possible effect of climatic deterioration. Journal of the Marine Biological Association of the United Kingdom 47: 81-95

Southward, A.J. (1991) Forty years of changes in species composition and population density of barnacles on a rocky shore. Journal of the Marine Biological Association of the United Kingdom 71: 495-513

Southward, A.J. and Crisp, D.J. (1954) Recent changes in the distribution of the intertidal barnacles *Chthamalus stellatus* Poli and *Balanus balanoides* L. in the British Isles. Journal of Animal Ecology 23: 163-177

Thieltges, D.W., Strasser, M., van Beusekom, J.E.E. and Reise, K. (2004) Too cold to prosper – winter mortality prevents population increase of the introduced American slipper limpet *Crepidula fornicata* in northern Europe. Journal of Experimental Marine Biology and Ecology 311: 375-391

Tøttrup, A.P., Chan, B.K.K., Koskinen, H. and Høeg, J.T. (2010) 'Flying barnacles': implications for the spread of non-indigenous species. Biofouling 26(5): 577-582

Urian, A.G., Hatle, J.D. and Gilg, M.R. (2010) Thermal constraints for range expansion of the invasive green mussel, *Perna viridis*, in the Southeastern United States. Journal of Experimental Zoology 313A: 1-10

Watson, D.I., O'Riordan, R.M., Barnes, D.K.A. and Cross, T. (2005) Temporal and spatial variability in the recruitment of barnacles and the local dominance of *Elminius modestus* Darwin in SW Ireland. Estuarine, Coastal and Shelf Science 63: 119-131

Wang, C., Liu, H. and Lee, S.K. (2010) The record-breaking cold temperatures during the winter of 2009/2010 in the Northern Hemisphere. Atmospheric Science Letters 11: 161-168

Wethey, D.S. and Woodin, S.A. (2008) Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. Hydrobiologia 606: 139-151

Wethey, D.S., Woodin, S.A., Hilbish, T.J., Jones, S.J., Lima, F.P. and Brannock, P.M. (2011) Response of intertidal populations to climate: Effects of extreme events versus long term change. Journal of Experimental Marine Biology and Ecology 400: 132-144

Witte, S., Buschbaum, C., van Beusekom, J.E.E. and Reise, K. (2010) Does climatic warming explain why an introduced barnacle finally takes over after a lag of more than 50 years? Biological Invasions 12: 3579-3589

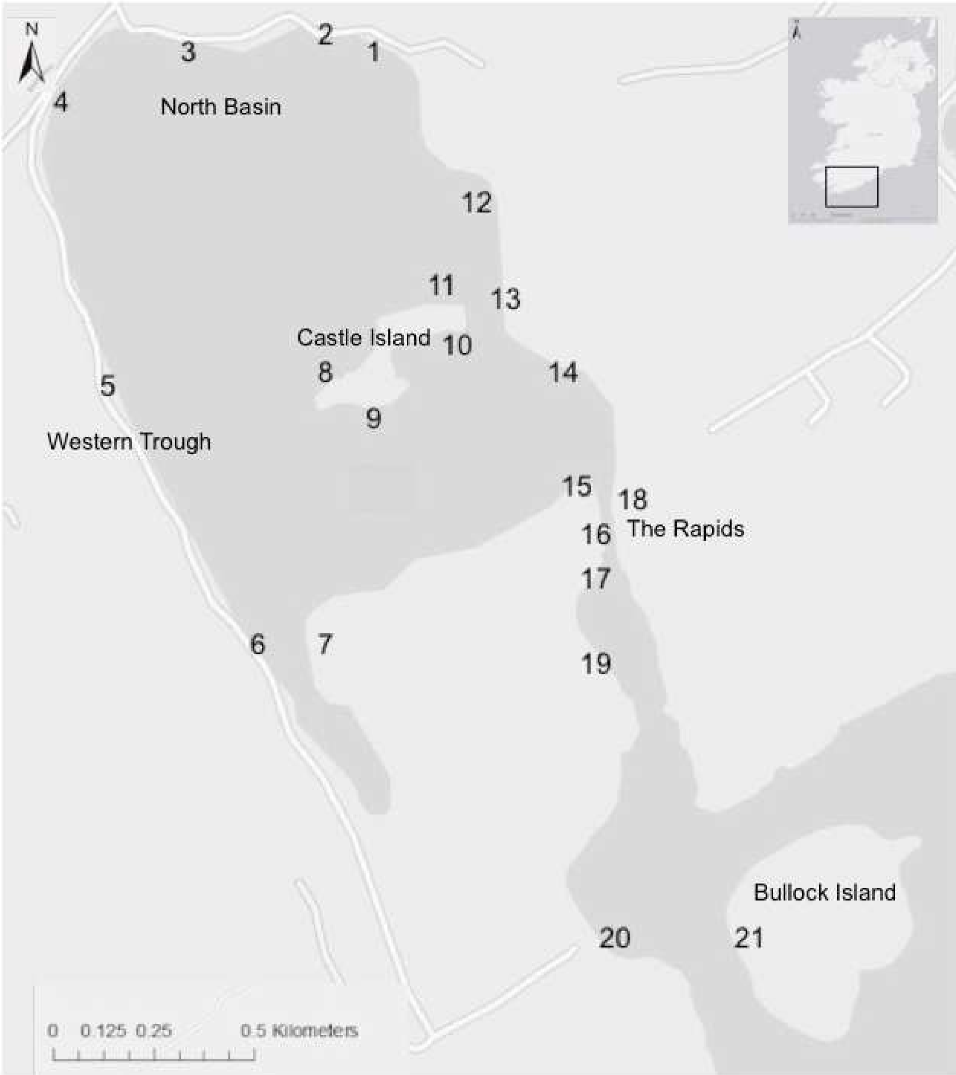

Figure 1. Map showing the location of study sites within Lough Hyne Marine Nature Reserve. For site details see Table 1. Inset map shows area enlarged.

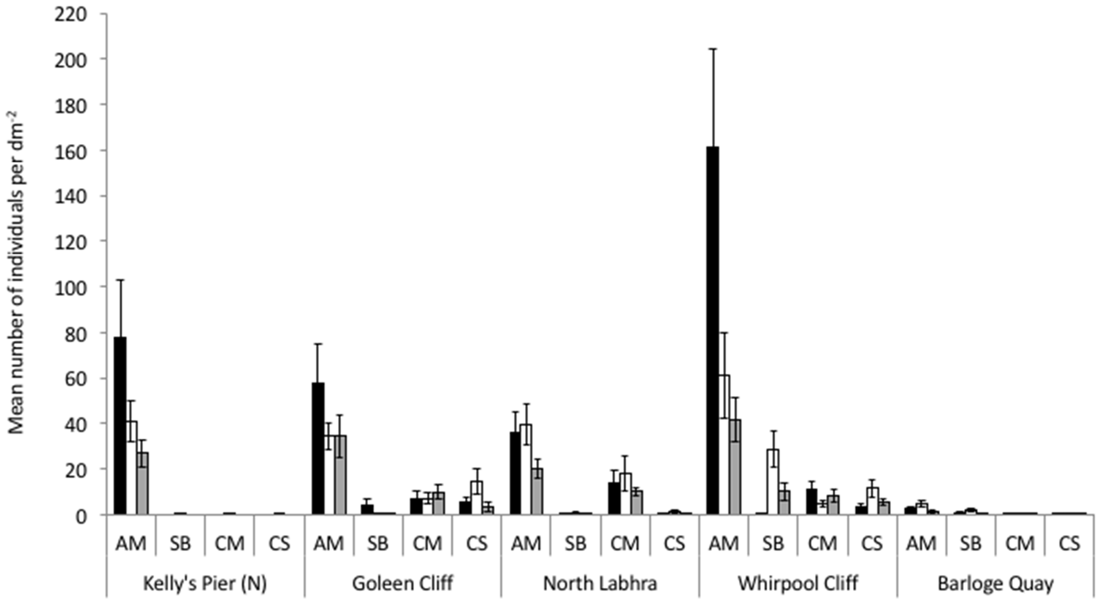

Figure 2. Mean number of individuals of four barnacle species *Austrominius modestus* (AM), *Semibalanus balanoides* (SB), *Chthamalus montagui* (CM) and *Chthamalus stellatus* (CS) recorded per dm^2 at five survey sites within Lough Hyne Marine Nature Reserve (Goleen Cliff, Barloge Quay, Kelly's Pier, North Labhra and Whirlpool Cliff) in 2009 (black bars), 2010 (white bars) and 2011 (grey bars). Error bars represent standard error.

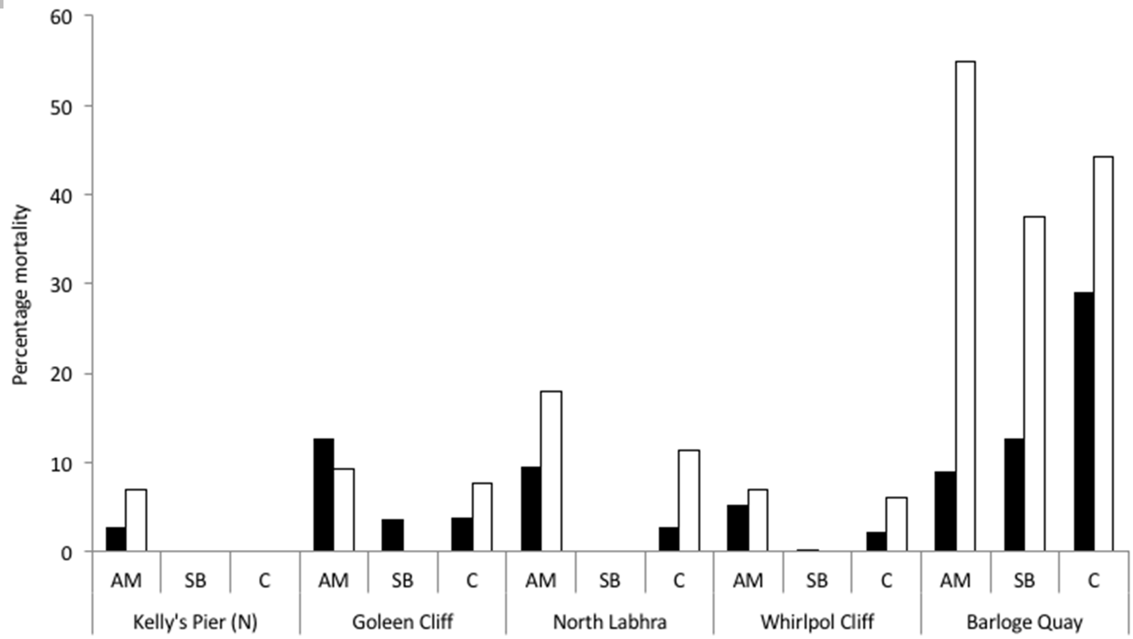

Figure 3. Percentage mortality of *Austrominius modestus* (AM), *Semibalanus balanoides* (SB) and *Chthamalus* sp. (C) recorded at five sites in Lough Hyne Marine Nature Reserve during the summers of 2010 (black bars) and 2011 (white bars).

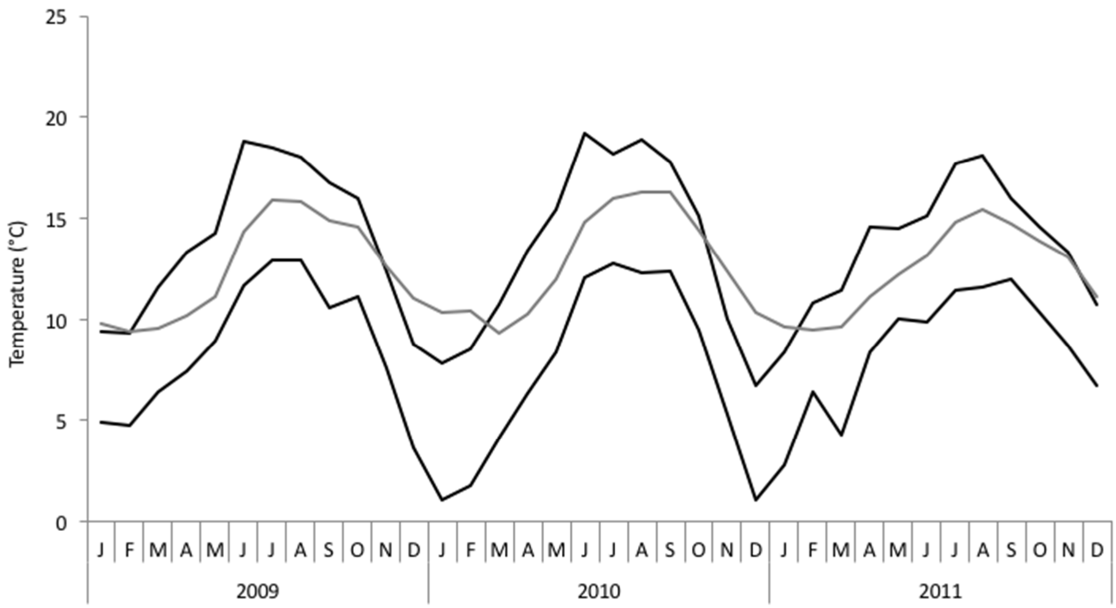

Figure 4. Mean monthly maximum (top black line), mean monthly minimum (bottom black line) from Sherkin Island weather station and mean monthly sea surface temperature (grey line) recorded from buoys M3 and M5 off the south coast of Cork from January 2009 to December 2011. Data obtained from Met Éireann.

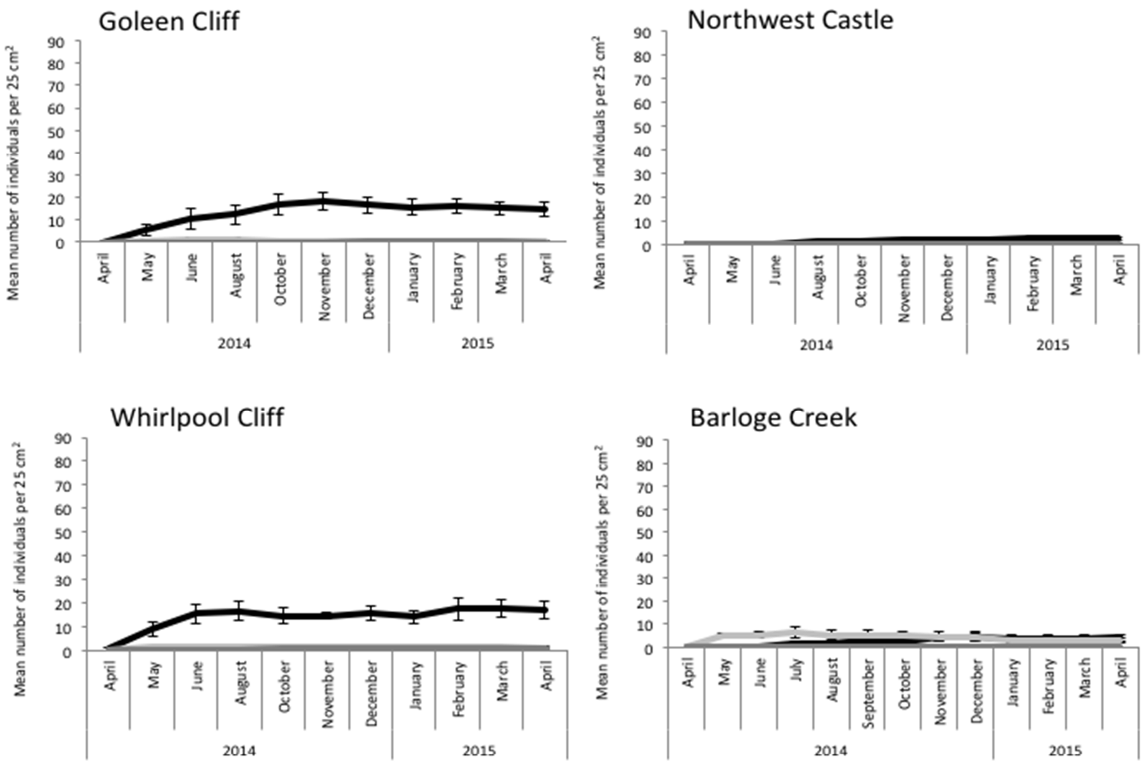

Figure 5. Mean number of recruits (± SE), per 25cm^2 free space, of three barnacle species, *Austrominius modestus* (black), *Semibalanus balanoides* (light grey) and *Chthamalus montagui* (dark grey), in removal plots at four sites, Barloge Creek, Whirpool Cliff, Goleen and Castle Island, within Lough Hyne Marine Nature Reserve from April 2014 to April 2015.

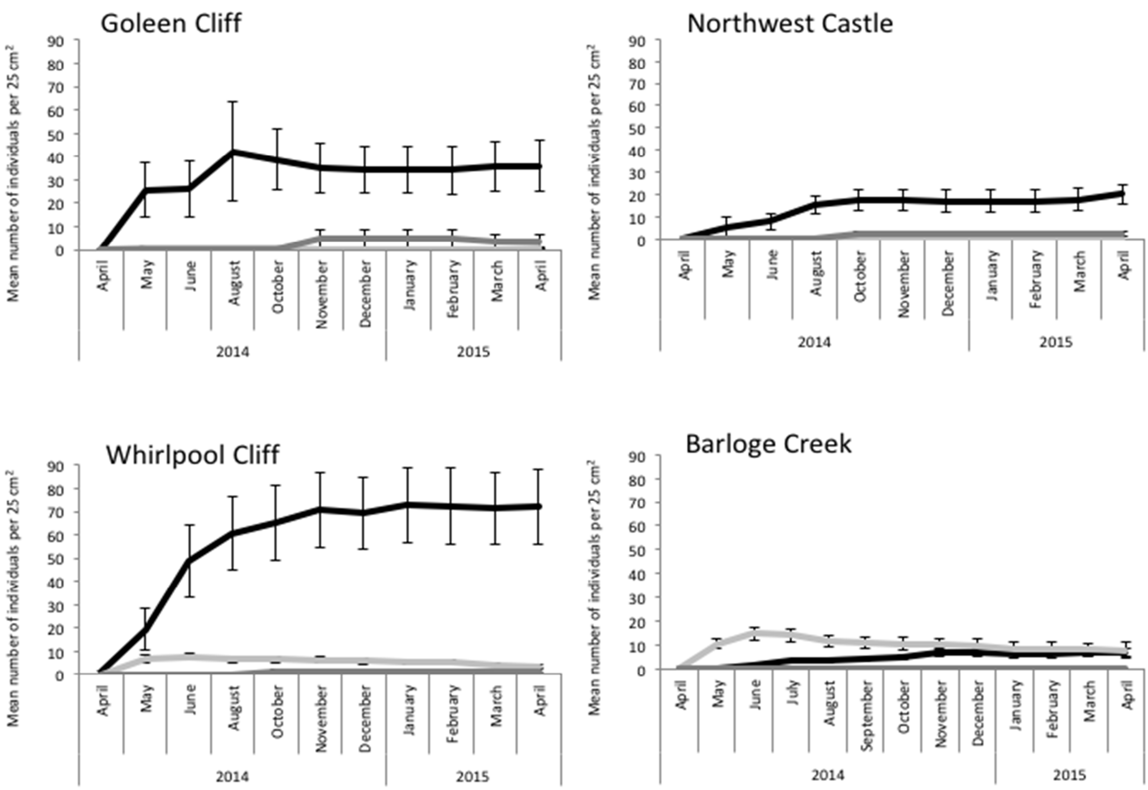

Figure 6. Mean number of recruits (± SE), per 25cm^2 free space, of three barnacle species, *Austrominius modestus* (black), *Semibalanus balanoides* (light grey) and *Chthamalus montagui* (dark grey), in control plots at four sites, Barloge Creek, Whirpool Cliff, Goleen and Castle Island, within Lough Hyne Marine Nature Reserve from April 2014 to April 2015.

Table 1. Name and GPS coordinates of survey sites within Lough Hyne Marine Nature Reserve. For site locations see Figure 1.

Site	Name	GPS
1	Gatehouse	N 51°29.518’ W 009°18.083’
2	North Wall	N 51°30.226’ W 009°18.106’
3	Freshwater Hill	N 51°30.221’ W 009°18.219’
4	Kelly's Pier	N 51°30.269’ W 009°18.476’
5	West Shore	N 51°30.031’ W 009°18.360’
6	Goleen	N 51°29.824’ W 009°18.147’
7	Goleen Cliff	N 51°29.880’ W 009°18.145’
8	North Labhra	N 51°30.078’ W 009°18.111’
9	Southeast Labhra	N 51°30.042’ W 009°18.001’
10	South Castle	N 51°30.069’ W 009°17.560’
11	Northwest Castle	N 51°30.081’ W 009°18.030’
12	East Shore Cliff	N 51°30.253’ W 009°17.966’
13	Castle Island Shallows	N 51°30.134’ W 009°17.885’
14	Whirlpool Cliff	N 51°30.041’ W 009°17.443’
15	Top of Rapids	N 51°29.595’ W 009°17.453’
16	Mid Rapids	N 51°29.591’ W 009°17.449’
17	Lower Rapids	N 51°29.568’ W 009°17.444’
18	Dromadoon	N 51°30.013’ W 009°17.724’
19	Barloge Creek	N 51°29.508’ W 009°17.455’
20	Barloge Quay	N 51°29.609’ W 009°17.695’
21	Bullock Island	N 51°29.613’ W 009°17.567’

Table A.1 Mean (± SE) number of individuals dm^{-2} of *Austrominius modestus* (AM), *Semibalanus balanoides* (SB), *Chthamalus montagui* (CM) and *C. stellatus* (CS) at twenty-one sites in Lough Hyne marine reserve in 2009.

	AM	SB	CM	CS
Gatehouse	32.5 ± 8.83	0.0 ± 0.00	3.7 ± 1.45	0.1 ± 0.03
North Wall	31.8 ± 7.46	0.0 ± 0.00	16.6 ± 3.80	3.2 ± 1.31
Freshwater Hill	30.6 ± 4.89	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
Kelly's Pier	77.5 ± 25.68	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
West Shore	52.7 ± 10.94	0.0 ± 0.00	11.9 ± 4.01	0.6 ± 0.30
Goleen	29.2 ± 9.92	0.0 ± 0.00	0.7 ± 0.44	0.0 ± 0.00
Goleen Cliff	58.0 ± 17.23	4.5 ± 2.12	7.3 ± 2.88	5.4 ± 2.54
North Labhra	36.4 ± 8.97	0.1 ± 0.11	14.1 ± 5.50	0.7 ± 0.29
Southeast Labhra	24.6 ± 4.76	0.0 ± 0.00	8.4 ± 2.71	1.5 ± 0.51
South Castle	28.1 ± 6.80	0.0 ± 0.00	9.2 ± 2.73	1.3 ± 0.36
Northwest Castle	0.4 ± 0.10	0.1 ± 0.01	0.1 ± 0.03	0.1 ± 0.02
East Shore Cliff	103.3 ± 26.84	0.0 ± 0.00	32.5 ± 7.05	6.0 ± 1.97
Castle Island Shallows	28.0 ± 8.35	0.0 ± 0.00	13.1 ± 3.38	0.3 ± 0.17
Whirlpool Cliff	161.5 ± 42.69	0.3 ± 0.18	11.3 ± 3.22	3.4 ± 1.26
Top of Rapids	20.6 ± 6.00	0.2 ± 0.11	2.5 ± 1.05	0.2 ± 0.08
Mid Rapids	5.9 ± 2.08	0.8 ± 0.42	40.0 ± 10.16	3.4 ± 1.06
Lower Rapids	8.3 ± 1.20	24.3 ± 4.58	13.4 ± 2.04	14.3 ± 2.22
Dromadoon	32.5 ± 5.34	0.1 ± 0.04	13.9 ± 4.77	1.5 ± 0.59
Barloge Creek	15.8 ± 2.73	1.4 ± 0.37	1.1 ± 0.21	0.8 ± 0.20
Barloge Quay	2.5 ± 0.60	1.0 ± 0.36	0.3 ± 0.07	0.1 ± 0.02
Bullock Island	10.2 ± 2.01	104.7 ± 16.32	33.8 ± 5.78	23.1 ± 4.34

Table A.2 “Prop.test” statistics comparing percentage mortality of each barnacle species at each study site at Lough Hyne in 2010 in comparison to 2011. Statistical analysis carried out using R Studio software (R Core Team, 2016).

	$\chi 2$	df	p
Kelly's Pier			
AM	55.84	1	< 0.001
SB	NA	NA	NA
C	NA	NA	NA
Goleen Cliff			
AM	12.53	1	< 0.001
SB	< 1	1	1
C	19.37	1	< 0.001
North Labhra			
AM	40.85	1	< 0.001
SB	NA	NA	NA
C	58.92	1	< 0.001
Whirlpool Cliff			
AM	6.69	1	< 0.001
SB	< 1	1	1
C	24.81	1	< 0.001
Barloge Quay			
AM	462.63	1	< 0.001
SB	35.19	1	< 0.001
C	5.4	1	< 0.05

Table A.3 Mean (± SE) number of individuals dm^{-2} of *Austrominius modestus* (AM), *Semibalanus balanoides* (SB), *Chthamalus montagui* (CM) and *C. stellatus* (CS) at twenty-one sites in Lough Hyne marine reserve in 2011.

	AM	**SB**	**CM**	**CS**
Gatehouse	6.6 ± 1.48	0.0 ± 0.00	17.9 ± 5.50	0.9 ± 0.46
North Wall	15.1 ± 2.71	0.1 ± 0.14	22.7 ± 4.71	2.0 ± 0.66
Freshwater Hill	28.2 ± 4.35	0.1 ± 0.15	0.2 ± 0.11	0.0 ± 0.00
Kelly's Pier	26.9 ± 5.90	0.0 ± 0.00	0.0 ± 0.00	0.0 ± 0.00
West Shore	29.8 ± 5.95	0.1 ± 0.08	11.2 ± 0.67	24.4 ± 6.48
Goleen	24.4 ± 6.48	0.1 ± 0.09	0.0 ± 0.00	0.0 ± 0.00
Goleen Cliff	34.5 ± 9.12	0.2 ± 0.18	10.0 ± 3.24	3.5 ± 1.75
North Labhra	20.0 ± 4.02	0.1 ± 0.05	10.1 ± 1.82	0.1 ± 0.05
Southeast Labhra	29.6 ± 7.56	0.0 ± 0.00	8.9 ± 4.13	2.1 ± 0.80
South Castle	24.7 ± 6.15	0.1 ± 0.08	9.2 ± 2.32	0.0 ± 0.00
Northwest Castle	24.1 ± 4.33	0.0 ± 0.00	5.4 ± 1.90	0.0 ± 0.00
East Shore Cliff	21.5 ± 4.40	0.3 ± 0.18	40.9 ± 11.93	1.8 ± 0.57
Castle Island Shallows	31.8 ± 7.98	0.1 ± 0.06	18.1 ± 4.58	0.1 ± 0.07
Whirlpool Cliff	41.7 ± 9.83	10.1 ± 3.65	8.2 ± 2.78	5.3 ± 1.40
Top of Rapids	4.4 ± 1.51	6.9 ± 1.83	26.8 ± 5.48	55.1 ± 3.06
Mid Rapids	2.7 ± 0.58	5.4 ± 1.73	17.1 ± 4.82	21.0 ± 4.47
Lower Rapids	3.0 ± 0.39	13.9 ± 2.12	17.4 ± 3.43	9.9 ± 1.27
Dromadoon	2.1 ± 0.49	2.7 ± 0.73	54.0 ± 9.00	40.8 ± 5.53
Barloge Creek	6.3 ± 1.19	0.8 ± 0.16	9.5 ± 2.34	1.1 ± 0.15
Barloge Quay	1.4 ± 0.53	0.6 ± 0.27	0.1 ± 0.06	0.3 ± 0.12
Bullock Island	1.9 ± 0.28	20.7 ± 4.01	32.3 ± 9.07	17.0 ± 2.61

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Table A.4 Zero inflated negative binomial model estimates for recruit data collected at Lough Hyne Marine nature reserve on a monthly basis from April 2014 – April 2015. Variables in bold italics represent the intercept value for comparison. Estimate values are log values. Statistical analysis carried out using R Studio software (R Core Team, 2016).

	Estimate	Standard error	z value	p
AM				
CM	-1.97	0.14	-13.81	< 0.001
SB	-1.50	0.09	-15.64	< 0.001
Barloge Creek				
Whirlpool Cliff	0.99	0.11	8.97	< 0.001
Goleen	1.30	0.13	9.78	< 0.001
Castle Island	0.76	0.15	4.43	< 0.001
AM control				
Remove	-1.20	0.11	-10.81	< 0.001
CM control	-2.77	0.12	-21.7	< 0.001
SB control	-0.64	0.14	-4.59	< 0.001
AM remove				
CM remove	-3.50	0.23	-14.82	< 0.001
SB remove	-0.38	0.14	-2.60	< 0.001